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Atlantic salmon in regulated rivers: Understanding river management through the ecosystem services lens

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Abstract

Known as the “king of fishes,” the Atlantic salmon (*Salmo salar*, Salmonidae) is an iconic freshwater species whose contribution to human well-being has long been recognized, as have widespread declines in its abundance, partly due to river regulation. To understand how salmon conservation has been addressed within the ecosystem services (ES) framework, we synthesized the peer-reviewed literature on ES provided by salmon in regulated rivers. We developed a search string to capture allusions to provisioning, regulating, supporting and cultural ES and assessed the results to identify knowledge gaps. The effects of hydropower on fisheries catches and on modelled populations were shown in several publications. Overall, few studies focused explicitly on ES from salmon and hydropower; this is surprising given the considerable body of literature on salmon in regulated rivers. Wild salmon as a food source and other provisioning services are less important today than historically. Because predators such as salmon are important for facilitating biodiversity by cycling nutrients and controlling food webs, there is a scope of work for future assessments of these regulating and supporting services. Few papers explicitly addressed cultural ES, despite the salmon's longstanding iconic status; this is a knowledge gap for future ES assessments in relation to hydropower. The influence of ES assessments for policy makers is growing through the Intergovernmental Panel for Biodiversity and Ecosystem Services (IPBES) and the post-2020 biodiversity strategy. Explicitly addressing ES poses an opportunity for river managers to raise awareness of aquatic conservation efforts and well-informed decision-making for sustaining ES.

KEYWORDS
cultural, hydropower, provisioning, regulating, *Salmo salar*, supporting

1 | INTRODUCTION

Ecosystem services (ESs) are defined as the benefits that people derive directly or indirectly from ecological processes, functions and characteristics; the general categories typically include provisioning, regulating, supporting and cultural services (Reid et al., 2005). The concept was first coined as "nature's services" in the late 1970s by Westman (1977), and the term "ecosystem service" was first used in the 1980s (de Assis Espécie et al., 2019). Assessment of ES can be considered as a resource management approach for decision-making, wherein valuation, mapping and integrated modelling of different ES serve as a method to recognize the importance of functioning ecosystems (Costanza et al., 2017). These assessments raise awareness about ES and provide detailed analyses of different policy choices where potential trade-offs exist (Braat & de Groot, 2012). Transdisciplinary (including economic) approaches for ES assessments may involve multiple stakeholders and have potential uses at various temporal and spatial scales (Costanza et al., 2017), and the ES framework has become the most widely used form of assessing the values of ecosystems for people since the publication of the Millennium Ecosystem Assessment (MEA; Reid et al., 2005). Nevertheless, the ES framework has received a considerable amount of critique (e.g. Schröter et al., 2014).

The ES concept and related assessments have been subject of debate and critique because of the anthropocentric, linear and economistic way of framing human–nature relations, with nature portrayed as a "service provider" (Schröter et al., 2014). Concerns include the fear that, despite the intentions related to sustainable management, the application of the concept will result in a reductionist understanding of ecology, how people value and interact with nature, as well as the importance of nature for society (Norgaard, 2010). Nonetheless, there is broad international support for developing much more comprehensive ES assessments under the umbrella of the Intergovernmental Panel for Biodiversity and Ecosystem Services (IPBES; Brondizio et al., 2019). The IPBES approach focuses on incorporating multiple stakeholders to understand the diverse values of biodiversity to foster sustainable management (Pascal et al., 2017). A relatively recently introduced expanded view on ES assessment is the concept of Nature's Contributions to People (NCP; Díaz et al., 2015; Hill et al., 2021; Kadykalo et al., 2019), which represents an inclusive interpretation of relations between human and nature with involvement of social sciences, humanities as well as local and indigenous knowledge in the work with environmental policy. NCP is now partly integrated into the IPBES conceptual framework, but IPBES has nevertheless been criticized for not including some key features of the NCP, for example, for not acknowledging that culture define all links between people and nature and the role of indigenous and local knowledge (Díaz et al., 2018). Regardless of the ongoing debate about its usefulness, the ES concept is still dominating as a means of integrating environmental, economic and social perspectives into policymaking, and, for example, the Convention for Biological Diversity's post-2020 Framework continues the focus on maintaining ES (CBD, 2021). Thus, we believe that fisheries managers have much to gain by engaging with the ES framework.

There is a current societal demand both to decrease carbon emissions through the use of fossil-fuel free energy sources and to conserve biodiversity. In this article, our aim is to synthesize the literature that specifically addresses the ES delivered by Atlantic salmon (*Salmo salar*, Salmonidae) in rivers regulated for hydroelectric power production. We focus on one of the world's most well-studied freshwater fish and a conservation flagship species, but we also hope to call attention to the potential for assessing ES for lesser known aquatic species.

The Atlantic salmon (hereafter *salmon*) is an iconic migratory fish species, highly valued for recreational and commercial fisheries (Aas et al., 2011; Netboy, 1968). Coined as "the king of fishes" by Izaak Walton (1653), salmon have a long and rich history among human cultures. The Atlantic salmon is native to Europe and eastern North America, and it has a complex and diverse life cycle that involves migration between marine (or lacustrine) and fluvial habitats for maximizing growth, survival and reproduction (Jonsson & Jonsson, 2011). Salmon populations contribute to human well-being directly and indirectly (Table 1) by providing a wide range of ES (Holmlund & Hammer, 1999; Kulmala et al., 2012). The species is extensively farmed for food and stocking, and wild populations were previously harvested commercially, but fisheries on remaining populations are today primarily recreational or for subsistence. In many areas, salmon form an integral part of the cultural heritage of people, and salmon rivers provide aesthetic values and various opportunities for recreation and tourism (Holmlund & Hammer, 1999; Myrvold et al., 2019). Also, salmon can provide important regulating and supporting ES. For example, they play a key role as predators in riverine food webs, as well as a food source for other aquatic

TABLE 1 Ecosystem services provided by Atlantic salmon categorized using the framework from MEA (Reid et al., 2005) and modified from Kulmala et al. (2012) and Harrison et al. (2018)

Provisioning services	Commercial harvest Subsistence harvest
Supporting and regulation services	Food web dynamics and nutrient cycling Sediment turnover and bioturbation Freshwater pearl mussel host
Cultural services	Regional, local and personal identity Cultural heritage Tourism opportunities Recreational and psychological values

(Andrews et al., 2018) and terrestrial (Merz & Moyle, 2006) species, and spawning salmon contribute to other ecosystem functions such as nutrient cycling (McLennan et al., 2019) and sediment turnover (DeVries, 2012).

Compared to other groups of fish, migratory freshwater fish are disproportionately threatened (Deinet et al., 2020), and wild salmon populations are severely depleted throughout its native range (Lenders et al., 2016; Limburg & Waldman, 2009). Freshwater habitat loss and fragmentation caused by, for example, river regulation are widely considered as two of the main drivers of historical population declines (other main drivers include climate warming, food web changes, overexploitation, diseases and parasites; Jonsson & Jonsson, 2011; Parrish et al., 1998). Hydropower constructions and dams act as barriers and hinder migration between essential habitats to complete the diadromous life cycle (Nilsson et al., 2005; Piccolo et al., 2012). In addition to creating passage problems and habitat fragmentation, hydropower operation may alter the flow and thermal regimes of rivers, affecting several life stages of salmon (Jonsson & Jonsson, 2011).

Both opportunities for renewable energy from hydroelectric generation and the conservation of wild fish populations are key issues for sustainable future use of rivers (Piccolo et al., 2019). The effects of hydropower operations and long-term development on ES provided by salmon (Butler et al., 2009; Kulmala et al., 2012) need to be described and analysed to make well-informed policy decisions on how to manage rivers from a holistic viewpoint. In this study, we synthesize peer-reviewed literature related to the effects of hydropower on ES from salmon in regulated rivers throughout its native range. Our objectives were to (1) categorize the services described in the literature into provisioning, supporting/regulating and cultural ES, using the framework of the Millennium Ecosystem Assessment (MEA; Reid et al., 2005; Table 1), and (2) synthesize the effects of hydropower on these ES.

1.1 | The diversity of hydropower projects

The need of electricity in modern society has increased tremendous during the last decades, and a sustainable use of renewable energy sources is crucial for future well-being. The development of hydropower for electricity generation must be conducted to minimize loss of other conflicting values, for example, the ES provided by salmon.

The scale and purpose of the hydropower plant influence both the capacity for electricity production and the potential impacts on ES provided by salmon. Hydropower is used for both base and peak load generation of electricity, and there are three basic types of hydropower plants. Typically, large hydropower systems use a high dam to store water in a reservoir that enables peak load generation (hydropeaking), whereas medium-sized and small systems often use either a diversion of a portion of the water through a canal to the hydropower plant or run-of-river operation where the natural flow determine the base load electricity generation (Egré & Milewski, 2002; Okot, 2013). The two latter types may or may not require damming of the river, but usually include some kind of water level control such as a weir, usually hindering upstream migration. In cases where the dam is located upstream of the spawning and rearing habitat, typically a minimum flow released into the channel is required to support the salmon population.

Whereas all rivers with dams that hinder migration require some kind of a fish passage solution to mitigate fragmentation, the hydropower plants that use a reservoir for peak load generation in addition affect the downstream environment by altering the flow and temperature regimes of the natural seasonal cycle. Additionally, hydropeaking regimes, where sub-daily rapid changes in discharge and periods of zero flow create unnatural fluctuations, have been associated with several negative ecological effects on fish, for example, stranding and altered food resources (Hedger et al., 2018; Moreira et al., 2019). Hydropower plants with large reservoirs may in addition affect the natural brackish layer dynamics in coastal areas (particularly in fjords) when the river regulation transfers freshwater outlet from the spring and summer to the winter, possibly affecting migration between marine and freshwater habitats (Johnsen et al., 2011).

The development of hydropower in rivers with Atlantic salmon differs to some extent among countries. The spread of water-mill technology before and during early modern period in Western Europe, as well as in the ninetieth centuries in North America, fragmented many rivers, leading to decline in salmon stocks (Dymond et al., 2019; Lenders et al., 2016). The development of large-scale hydropower began around 1900, with most hydropower plants built in the 1940s, 1950s and 1960s (Forseth et al., 2017; Moran et al., 2018; Perers et al., 2007).

Impassable hydropower dams is perhaps the main reason for extirpation of salmon populations throughout its entire native range, particularly when the dams are located in the lower main-stem (Parrish et al., 1998). Dams hinder and delay salmon migration

(Thorstad et al., 2008) even where fishways may provide passage opportunities. The efficiency of fish passage solutions varies, and their performance in passing up- and downstream-migrating salmon seems to be idiosyncratic to some extent (Nyqvist et al., 2017). Factors such as river length, numbers and type of barriers, functionality of fish pass solutions (or lack thereof) play major roles, and multiplicative effects of several small migration obstacles may hinder natural migration completely (Piccolo et al., 2012). Several publications describing the connection between migration barriers and the worldwide decline of salmon were published before 2006 (e.g. Kazakov, 1992; Mathers et al., 2002; Parrish et al., 1998; Ritter, 1997), and these papers were thus not included in our search results.

1.2 | Ecosystem services provided by Atlantic salmon in regulated rivers

The most commonly used definition of ecosystem services is offered by the MEA: "the benefits people obtain from ecosystems" (Reid et al., 2005). Here, ecosystem services are divided into the categories of provisioning, supporting, regulating and cultural services, all of which arise from properties of ecosystems. Categorization and assessments of ES can be carried out to give an overview of a system, but are usually carried out in relation to a policy or land-use change, which affects the different flows of ES. Since ESs are usually categorized and analysed in relation to a beneficiary, the outline of ecosystem services in a given ecosystem varies depending on the analysis and issue at stake (Haines-Young & Potschin, 2010). Sometimes benefits and processes can be considered for multiple ES categories; for example, recreational fishing can be considered as both a cultural ES (such as a community-strengthening practice and psychologically rewarding recreational activity) and a provisioning ES (if the catch is consumed). For people living near a salmon river, the species that historically was important for providing food can function as a symbol for local identity (Figure 1), it can attract tourism, and traditional fisheries may constitute a part of local cultural heritage.

The provisioning services Atlantic salmon once provided through commercial and subsistence fishing have diminished with declining wild populations, and the monetary value of recreational fishing in coastal areas and rivers (providing mainly socio-cultural services) is likely higher today (Myvold et al., 2019). Wild salmon, as well as hatchery-reared salmon stocked to support the fisheries, are prized fish among anglers, and salmon populations are key assets for many regions' income from the sport fishing sector. In a recent review on social, economic and cultural values of salmon, Myrvold et al. (2019) compiled information from several year and different countries about the total expenditure per day for salmon anglers, which ranged from 100 to 600 €. Although these types of studies can show an indication of monetary value of, for example, recreational fishing, it does not specify which ES category that provides for the benefit that users are willing to pay for. In order to delineate what type of ES is provided by Atlantic salmon, more comprehensive analyses that consider all four categories of ES, and the potential interlinkages and overlaps between them, are required.

Pacific, semelparous salmonid species have been proven to provide the supporting ES of transporting crucial marine-derived nutrients to freshwater ecosystems and their surrounding riparian zones (Gende et al., 2002). Atlantic salmon are iteroparous, but between 20% and 100% of the adults nevertheless die after spawning (Nyqvist, 2016), and their carcasses may constitute a relevant nutrient addition for many rivers (McLennan et al., 2019). Moreover, during and after spawning, Atlantic salmon gametes are eaten by riverine organisms (Samways et al., 2017), also contributing to the linkage between the marine and freshwater ecosystems.

Salmon functions as a key consumer species at its juvenile life stages, and they occupy a niche as a drift-feeding predator of aquatic invertebrates in fast-flowing river stretches (Heggenes, 1990). In many northern rivers, this niche may overlap with those of other salmonids. The riffles with the fastest water velocities, however, are usually used only by salmon parr (Riley et al., 2009). In this environment, salmon is likely one of few species that can control the food web dynamics by regulating the production of drifting aquatic invertebrates (Poff et al., 1998). Salmon thereby mediate competition

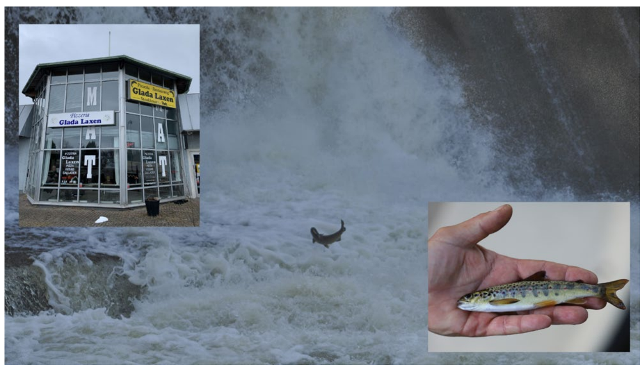

FIGURE 1 A landlocked Atlantic salmon spawner leaping in the rapids of the River Gullspång, Sweden, just below the hydroelectric dam that has been a complete migration barrier since the early 1900s (Lund Bjørnås et al., 2021). Landlocked salmon have been migrating up the River Gullspång since the glacial ice retreated from southern Sweden some 9000 years ago. The Gullspång salmon is renowned as the world's largest-bodied landlocked salmon with weights up to 20 kg, and it has long been a symbol for place-based identity and local pride for the people of Gullspång municipality. Top left inset is the sign for the "The Happy Salmon" pizza shop, known to all who drive past the town. Bottom right inset shows a salmon parr in the hand of a biologist, during the annual population monitoring. Largely through the initiative of local biologists, a co-management program with multiple stakeholders has developed over a > 50 year period, aiming to ensure sustainability of the population in the face of long-term hydroelectricity production. The future is far from certain for this salmon population, but through the efforts of dedicated stakeholders, the Gullspång salmon still have a fighting chance. Their future is literally and figuratively in our hands

between invertebrate species and possibly support the ecosystem by upholding biodiversity.

During spawning, salmon excavate the riverbed to produce redds. In stretches with high density of spawners during autumn, this bioturbation potentially contributes to sediment turnover and cleans the bottom substrate from organic material (Field-Dodgson, 1987). The digging of redds potentially also increases invertebrate drift that temporarily become accessible to conspecific juveniles and other drift-feeding animals (Minakawa & Gara, 2003). The effects of river regulation on the flow regime per se likely play an overriding role in sediment transport and dynamics than its indirect effect on the supporting ES from salmon turning over sediment when digging redds (Batalla et al., 2021). A natural annual flow cycle, with, for example, spring floods, normally flushes coarse material clean from silt, whereas a regulated river may have both more extreme flows (typically at other times as the naturally occurring floods) and a lack of high-flow periods, resulting in an altered sediment dynamic.

Next to the congeneric brown trout, salmon functions as an important host species for the freshwater pearl mussel (*Margaritifera margaritifera*, Margaritiferidae). This endangered mussel (IUCN Red List) is often targeted in river restoration actions (Geist, 2010). The freshwater pearl mussel also provides a range of ES (Vaughn, 2018), and it has been, for example, historically and culturally important for providing pearls for jewellery. Freshwater pearl mussel larvae are parasitic and must find hosts by attaching to fish gills and live as an ectoparasite, until they detach and start growing as a juvenile mussel (Hastie et al., 2000). Salmon and freshwater pearl mussel are often both targeted species in aquatic conservation programs for riverine ecosystems in the northern hemisphere (Geist, 2015), and effects of river regulation of salmonid population dynamics may therefore directly influence the recruitment of juvenile mussels (Österling & Söderberg, 2015).

2 | METHODS

For the literature search, we used the Web of Science Core Collection, which accessed the following databases using the Karlstad University library subscription: Science Citation Index Expanded (1900–present), Social Sciences Citation Index (1956–present), Arts & Humanities Citation Index (1975–present), Conference Proceedings Citation Index - Science (1990–present), Conference Proceedings Citation Index - Social Science & Humanities (1990–present) and Emerging Sources Citation Index (2015–present). We used the field tag TS (topic) for our search string (Table 2), which was created broad enough to find most publications that dealt with ES of salmon in relation to hydropower. We built our search string so that the results would consist of scientific publications that included salmon, ES and hydropower. We used the words [salmon* OR "salmo salar"] so that we would not miss papers that in had a general salmonid focus (i.e. including Atlantic salmon) or regional scientific papers about Atlantic salmon that did not use the name Atlantic (but instead for example Baltic salmon). For the ES part of the search string, we aimed at a broad range of words connected to different ES provided by salmon (Kulmala et al., 2012). The last part of the string was built from words that specifically were connected to hydropower. To reduce the number of irrelevant papers found, we actively chose not to include those dealing with salmonella, gene regulation and beaver dams. The time span for the search was restricted to 2006–2020 (i.e. after the Millennium Ecosystem Assessment; Reid et al., 2005). Using this search method, we aimed at finding publications that directly discussed hydropower generation and ES provided by Atlantic salmon, and the scope of the results in this study is thus limited to a synthesis of the recent body of literature that includes both these two areas.

The initial search (Table 2) resulted in 1574 papers. In a first screening (Figure 2), we excluded papers that clearly did not deal with Atlantic salmon by reading the abstracts, which resulted in 311 papers kept for a second screening. We read these papers and excluded those that were not related to our study (for example, those with focus on fish behaviour, habitat use or physiology). This second screening resulted in 106 papers, which we read in detail during the third screening (Figure 2). In addition, we made a search (Table 2) in the SCOPUS database, but we found no additional relevant publications.

TABLE 2 Search criteria for the selection of publications for related to ecosystem services provided by Atlantic salmon in rivers with hydropower regulation and published between 2006 and 2020

Feature	Search criteria
Publication database	ISI Web of Science (Core collection) – Advanced search
Search field	TS=topic. Searched for terms in Title, Abstract, Author Keywords & Keywords Plus®
Search string	TS= ((salmon* OR "salmo salar") AND (provision* OR food OR fisher* OR "genetic resource*" OR "habitat form*" OR "habitat creat*" OR regulat* OR support* OR "nutrient cycl*" OR "food web" OR "food chain" OR "indicator*" OR "water quality" OR "socioeconomic" OR "top down" OR "biodivers*" OR cultur* OR recreat* OR spirit* OR aesthetic* OR education* OR angl* OR inspiration* OR touris* OR valu* OR "ecosystem function*" OR "ecosystem process*" OR "ES*" OR people OR soci*) AND (dam* OR hydropower* OR hydroelectric* OR HEP OR "river regulation" OR "regulated river*") NOT "salmonella" NOT "gene regulat*" NOT beaver)
Time span	From 2006 to 2020

In the third cut, we included the papers involving ES provided by salmon in relation to hydropower. We also included papers that did not explicitly use the term *ecosystem service* but instead discussed the use of wild Atlantic salmon for humans, ecosystem functions and/or processes or had population-level data on salmon in relation to hydropower. This third screening left us with a final sample of 33 publications (Figure 2; Table S1) that were assessed. We categorized each paper according to publication year, country of origin (based on first author affiliation and salmon population) and the MEA ES categories (Table 1). We categorized publications that discussed the effects of hydropower on salmon population development separately from those that explicitly linked their discussion to an ES category, because effects on population viability should affect all ecosystem services provided by salmon. The relationship between salmon population density and the quantity and quality of different ES is not necessarily linear however, in particular relationships with cultural ES.

3 | RESULTS

Half of the 33 papers that we included were published during the last five years (2016–2020) in the time span of our literature search. Before this span (i.e. 2006–2015), there was on average one to two included papers from each year (Figure 3). Most studies originated from Scandinavia, with Norway being the country with the highest number of included papers, in terms of both first authorship and origin of salmon population studied. The Scandinavian countries (except Denmark) have numerous salmon rivers, and hydropower constitutes a major electricity source in their power mixes (Norway: ~95%; Sweden: ~50%; Finland: ~20%). The number of included papers from North America was similar to that of papers from Western Europe. There was also one included paper from Russia (Figure 4). The majority of the included papers dealt with effects on population development. Ten papers focused explicitly on the role of salmon as provider of regulating, supporting and provisioning ES in regulated rivers. No paper dealt exclusively with cultural ES, but some papers discussed these services together with other services and population development in relation to hydropower (Figure 5).

3.1 | Population development and fisheries catches

Our literature search resulted in several papers on population modelling that indicated a negative relationship between hydropower dams and population development, an effect primarily caused by reduced migration success for both upstream-migrating spawners (Lundqvist et al., 2008) and downstream-migrating smolts and kelts (Lawrence et al., 2016). In addition to migration obstruction, rapid dewatering of shallow areas at hydropeaking flow regimes may

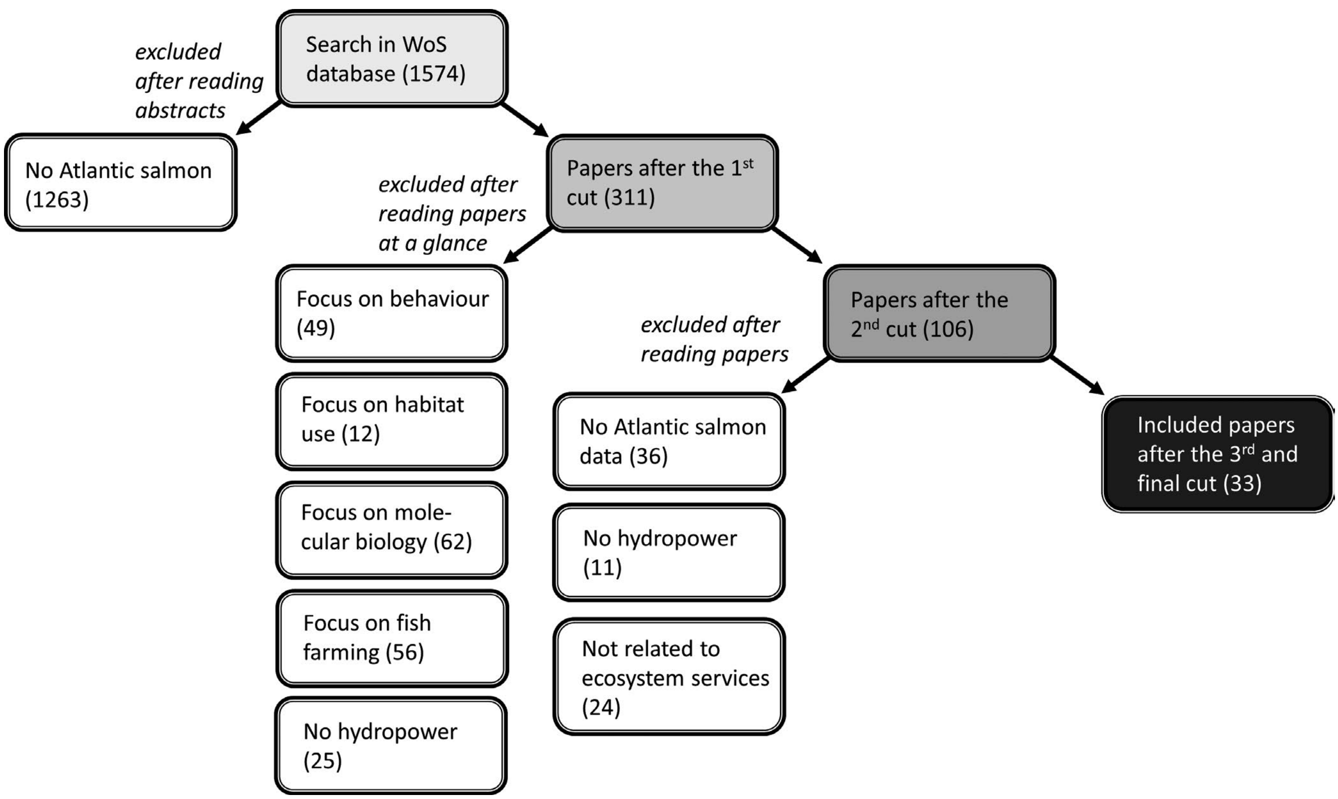

FIGURE 2 A schematic figure showing the screening of papers related to ecosystem services provided by Atlantic salmon in rivers with hydropower regulation and published between 2006 and 2020. White boxes represent excluded papers with text indicating the reason for exclusion. Numbers within parentheses indicate the number of papers

result in stranding of juveniles, which may have negative effect of population growth (Sauterlaute et al., 2016). Density-dependent mortality, however, may compensate for this effect of stranding (Hedger et al., 2018), and the general importance of stranding for salmon populations in regulated rivers remains unclear.

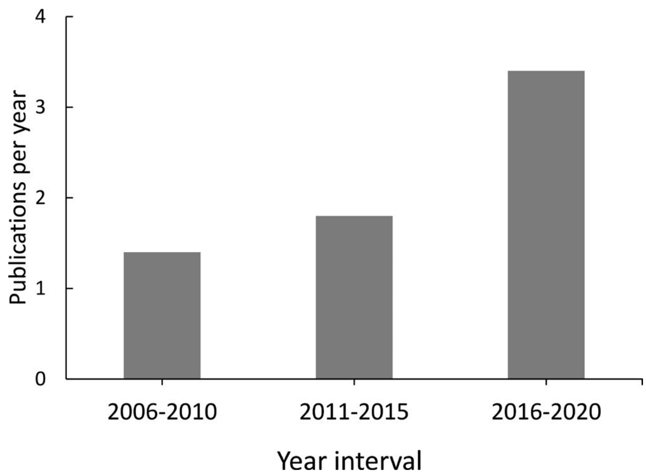

FIGURE 3 The distribution of publication year for the 33 papers included in the study

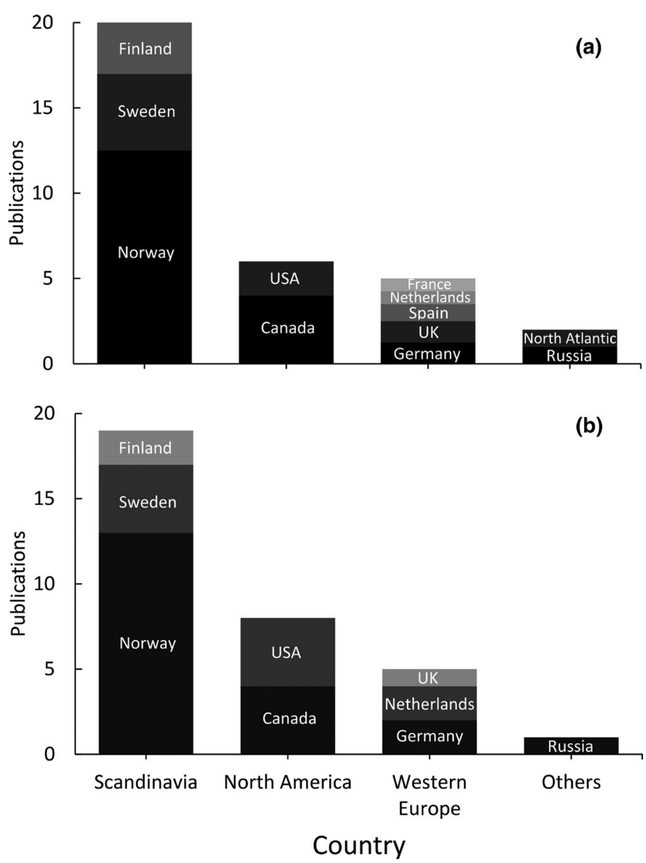

FIGURE 4 The origin of (a) the Atlantic population studied and (b) the publication (based on first author affiliation) of the 33 papers included in the study

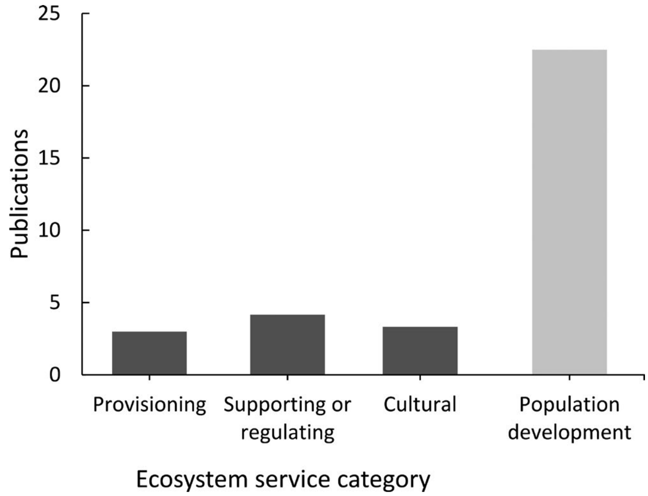

FIGURE 5 The ecosystem service category (Reid et al., 2005) of the cases reported in the 33 papers included in the study. Papers dealing with effects on population development and not explicitly an ES category are represented in its own category as a (light grey) bar to the right. When papers dealt with multiple categories, those papers were fractionalized between the categories

The trade-off between optimal electricity generation and the support of habitat for spawning and rearing of salmon has been debated extensively, because periods with low discharges are considered as hydrological bottlenecks for salmon populations (Adeva-Bustos et al., 2019). Most hydropower plants are obliged to release some water to obtain a minimum flow downstream of the dam, and the amount of water released at a given time ideally has some foundation in the natural flow regime. The natural pristine flow regime is often unknown, however, or cannot be combined with cost-efficient electricity production. Modelling tools may thus be used to analyse scenarios with different minimum flows to evaluate their effects on population development. The magnitude of flow and smolt production of a river are generally linked (Adeva-Bustos et al., 2019; Barton et al., 2020). However, this positive relationship usually does not manifest over the entire range of possible flow regimes proposed (Adeva-Bustos et al., 2017). Nevertheless, if river flow rates fall below a (sometimes unknown) limit, there are typically large negative effects on salmon populations, which is indicated by both simulations (Adeva-Bustos et al., 2019) and fisheries catches (Saltveit et al., 2019).

Although in silico modelling can be a useful tool to investigate how hydropower development and operation affect salmon populations and fisheries catches, our search resulted in twice as many papers connected to salmon abundance or fishing based on empirical fisheries data (12) than on simulations (6). Historical documents with information about fisheries catches and market supply of salmon show that dams constructed from when watermill technology was the only hydropower used and later, have substantially contributed to the steep decline in salmon, in both North America (Bowlby et al., 2016; Dymond et al., 2019; Limburg & Waldman, 2009; Morrison, 2019) and Europe (Erkinaro et al., 2011; Forseth et al., 2017; Lenders, 2017; Lenders et al., 2016; Limburg & Waldman, 2009; Piccolo et al., 2012; Saltveit, 2006; Soininen et al., 2019).

In rivers where spawning grounds mainly are located downstream of the lowermost dam, hydropower operation may have ambiguous effects on fisheries catches. L'Abée-Lund et al. (2006) compared fisheries catches before and after hydropower development in multiple Norwegian rivers. They did not find a general trend that hydropower reduced fisheries catches, and surprisingly, they instead suggested potential positive effects of hydropower, possibly as a result of some rivers increasing their minimum winter flow and reducing the spring flood after regulation. The development of hydropower in many cases was difficult to separate from other factors, however, such as gravel removal and stocking with hatchery-reared fish (L'Abée-Lund et al., 2006; Saltveit, 2006). Contrastingly, electrofishing catches data on juvenile densities in Norwegian rivers indicate that rivers generally have higher densities without than with hydropower development (Hesthagen et al., 2011).

The flow regime of a river system influences several life stages of salmon. Because hydropower electricity generation normally modifies the flow regime, fisheries catches of salmon in regulated rivers can likely be influenced by how the plants are operated, although the population response to different flow regimes may be complex. For example, the angling catches of one-sea-winter spawners are positively associated with discharge during upstream migration, but this correlation is weakened in rivers with hydropower (Otero et al., 2011). Further, distance between the dam and the spawning and rearing sites may play an important role in mediating potential effects of hydropower river regulation (Ugedal et al., 2008), which further complicates the picture. All in all, obstructing migration routes has long-term negative effects on fisheries catches, but how flow regimes downstream of hydroelectric power plants should be designed to achieve sustainable fisheries needs to be investigated further.

The conception of hydropower dams as posing a threat to salmon fisheries may not be widely spread among the lay public. For example, from interviews with anglers in a Spanish river, Juanes et al. (2012) concluded that only 10% of the respondents identified dams as a main cause of the decline of salmon. In four European countries (France, Germany, Norway and Sweden), two studies using questionnaires shed light on the public's view on hydroelectric generation in relation to salmon abundance (Kochalski et al., 2019; Riepe et al., 2019). Regardless of nationality, the respondents had little concerns regarding potential negative effects of hydropower plants on fisheries (Kochalski et al., 2019). Yet, people were willing to pay between 9 and 100 € per person and year to reach a more free-flowing river system state and between 40 and 150 € per person and year to have salmon in the river (Riepe et al., 2019). In a case study from northern Sweden, Håkansson (2009) evaluated how much the lay public was willing to pay for increased salmon abundance. In a scenario where hydroelectric generation was operated to increase the potential number of yearly spawners from 3000 to 4000, she assessed that this adjustment must cost less than 10–52 million € for the new operation to be profitable in the view of the public. The estimated cost of lost electricity production in the scenario corresponded to 25–70 million € with today's electricity price in Sweden (~0.05 €/kWh).

Studies based on stated preference methods that assess the value of salmon to the lay public, however, only account for partial value of the ES provided. Instead of assessing the monetary value of salmon to people based on willingness to pay, direct ES (such as fisheries opportunity) and indirect services (such as enabling angling tourism), using a stratified analysis between diverse stakeholders and different users, can yield more comprehensive results (Karjalainen et al., 2013).

3.2 | Provisioning ecosystem services

Most publications focusing on historical effects of river regulation on fisheries catches indirectly deal with provisioning ES, e.g. salmon as providing food and material for clothing, whereas more contemporary effects likely have implications mainly for other categories of ES, and it may be difficult to disentangle them. There were, in addition, publications that dealt with provisioning ES more directly. Hydropower potentially affects the flooding of reservoirs, which may lead to a pulse of methylmercury, which can accumulate in riverine fish such as salmon (Calder et al., 2019), reducing the value for consumption. Moreover, wild salmon populations have been essential for providing the fish farming industry with genetic material, but few studies have investigated how hydropower dams affect the genetic diversity. Although it is well known that damming has extirpated many locally adapted populations (Forseth et al., 2017), there is little research conducted that explores how within-population genetic diversity is affected by hydropower (Johnsen et al., 2014). Moreover, hydropower does not seem to influence the probability of spawners ascending other rivers than those in which they were born (i.e. straying; Bowlby et al., 2016), a phenomenon that maintains gene flow between populations and thus may preserve genetic diversity.

3.3 | Regulating and supporting ecosystem services

Few papers have investigated how hydropower dams affects ES related to food web dynamics and nutrient cycling by salmon. In our literature search on ES provided by salmon in relation to river regulation, we found three papers mentioning the role of salmon in the food web and as transporter of marine-derived nutrients to freshwater systems (Guyette et al., 2014; Karjalainen et al., 2013; Lenders et al., 2016). One of these based its discussions on original quantitative data (Guyette et al., 2014). The role of salmon in providing these ESs seems to be understudied, in particular the aspects of food web dynamics control.

Guyette et al. (2014) used historical data on quantity and timing of salmon runs and their carcass-based delivery of marine-derived nutrients to the headwaters of a former salmon river (Penobscot River, USA). The authors added carcass analogues to simulate the nutrient addition that dead post-spawners would subsidize should the river have no barriers to migration. In the study, salmon fry were also stocked in the system, and the effect of the nutrient addition was assessed by stable isotope analysis showing that stream macroinvertebrates and the salmon fry assimilated more than half of both the nitrogen and carbon. The proportion of assimilated added material depended on the functional feeding group of the organisms. The study thus supports the view that migration barriers decouple energy and nutrient fluxes between marine and freshwater environments by blocking migration routes for anadromous species such as salmon. It is difficult to assess the importance of this ES provided by salmon, and nutrient cycling has not yet been studied using, for example, a value-focused multi-criteria analysis framework (Karjalainen et al., 2013). We found no paper that quantified the importance of salmon bioturbation in relation to the effects of river regulation on sediment turnover, and we agree with, for example, Karjalainen et al. (2013) that this ES provided by salmon has probably minor significance.

The link between salmon and freshwater pearl mussel in relation to hydropower was discussed in four papers from our literature search (Addy et al., 2012; Bespalaya et al., 2007; Karjalainen et al., 2013; Soininen et al., 2019). None of these papers quantitatively assessed how river regulation indirectly affected freshwater pearl mussel recruitment through effects on salmon as mussel host. The monetary value per specimen of freshwater pearl mussel has been assessed at approximately 600 € (Karjalainen et al., 2013), and the ES provided by salmon functioning as a host is hence potentially important in river systems with hydropower.

3.4 | Cultural ecosystem services

Out of seven papers that mentioned cultural ES, only two explicitly included this ES category (Barton et al., 2020; Karjalainen et al., 2013), whereas the rest mentioned (alongside other topics) the social and cultural aspects and benefits associated with salmon. These mentions reflect the notion that cultural benefits are often integral to resource and ecosystem management. The cultural aspects are often overlooked, however, because fisheries research in general has mainly focused on ecology and harvest potential and less so on social aspects. The seven papers had different framings, methods and materials as to how they discuss cultural ES, which highlights the challenges of comparing empirical findings of the impacts of hydropower.

Morrison (2019) provided a chronology of salmon in Lake Ontario, and the species has formed part of local communities' subsistence and recreational fishing, cultural heritage and narratives of the area from the 1600s and onwards, all of which have been affected heavily by the construction of dams. Piccolo et al. (2012) assessed the current status of the Swedish Lake Vänern's remaining salmon and trout (*Salmo trutta*, Salmonidae) stocks and the importance of fisheries since the late 1800s and its relation to hydropower. Sport fish catch in Lake Vänern has increased from 30 to 80 t during the period of 1986 – 2006, indicating that the main fisheries has shifted from commercial to recreational, which is a growing activity and an asset in the area (Andersson et al., 2020). Salmon can also form integral parts of indigenous cultures' heritages. One paper mentioned the importance of salmon as a traditional food for Inuit people and how hydropower may affect the future usage of this resource in relation to public health issues (Calder et al., 2019).

The papers that explicitly included cultural ES (Barton et al., 2020; Karjalainen et al., 2013) focused on multi-criteria decision analyses. Barton et al. (2020) developed methodology based on Bayesian networks to assess trade-offs between hydropower production, recreational salmon fishing and riparian landscape aesthetics, as well as habitat quality. Riverscape aesthetics and experiences from recreational angling were assessed through expert-based models, and the authors found that weir removal and environmental flows had a large positive impact on fishability, but less on aesthetic value of the riverscape. Karjalainen et al. (2013), on the other hand, investigated how an ES approach for assessing restoration options of regulated rivers in Finland compares to a value-focused approach with regard to criteria and attributes, and to what extent ES can be seen to take stakeholder and societal values into account. Here, cultural ES included local identity and amenity values, tourism and recreational fishing, and assessments included a constructed scale (local identity) and economic contingent valuation method (recreational fishing).

Overall, the result from our search reveals lack of research attention to social and cultural aspects and stakeholder involvement associated with the management of regulated rivers. Erkinaro et al. (2011) outlined the importance of social aspects (alongside that of biological and technical ones) of restoring salmon populations in regulated rivers in northern Finland. Historical ignorance to local social impacts and stakeholder involvement in hydropower development emphasize the role of multidisciplinary collaboration, networking and social capital in restoration projects (Erkinaro et al., 2011). Fishery interests have become increasingly heterogeneous in this area, including not just commercial but recreational and scenic values, and inhabitants see salmon as an essential element in developing local tourism. Historically, there has been a lack of consideration to social–ecological systems in relation to hydropower operations in Finland, resulting in legislation and management underemphasizing impacts of hydropower on the river ecology (Soininen et al., 2019), and the multifunctionality of the services provided by river ecosystems (including cultural ES) has to be highlighted. Karjalainen et al. (2013) point out that the attempts to use the scientific concept of ES to understand social values and to communicate with stakeholders are potentially problematic or unfitting.

4 | DISCUSSION

Producing renewable electricity from hydropower while maintaining riverine biodiversity remains a critical issue for the future sustainable management of rivers. With increased emphasis on fossil-fuel free energy, scientists are likely to find their research on sustaining fish populations coming to the forefront of policy decisions about the complex trade-offs among competing aspects of sustainability. Explicitly describing and assessing the ES provided by such flagship species as salmon may provide essential information for managers and policy makers (Karjalainen et al., 2013); in particular, taking account of the importance of these species beyond the monetary values may play an increasingly important role. In our synthesis of peer-reviewed research papers published between 2006 and 2020, we discovered that the links between hydropower and Atlantic salmon population development and fisheries catches have been documented to a reasonable extent, whereas how hydropower explicitly influences ES provided by salmon has not. Two main services that potentially have been overlooked as major factors for the value of a hydropower-regulated salmon rivers are the role of salmon in the ecosystem (1) as controlling and facilitating biodiversity, for example, by providing marine-derived nutrients (Guyette et al., 2014), functioning as key predators in food webs in habitats with fast flowing water and acting as host for freshwater pearl mussels, and (2) as an iconic species, providing value to cultural heritage, recreation, aesthetics and tourism (Aas & Onstad, 2013; Myrvold et al., 2019). These services may well be described in the scientific literature, but not explicitly in relation to hydropower. Previous reviews focusing on ES from regulated rivers (e.g. de Assis Espécie et al., 2019) generally include fish mainly as a provisioning service and fail to recognize other important types of ES including supporting, regulating and cultural services, perhaps because of the difficulties to assign monetary values to them (Myrvold et al., 2019). Furthermore, the relationship between population density and the quantity and quality of these provided services is unclear and may be difficult to elucidate, but should nevertheless be evaluated.

Attempts to conceptualize the ways that a species such as salmon is of importance to people in terms of ES sheds light on the more general problem of a potential reductionism involved in fitting complex social–ecological relationships to the framework and categories of ES. Of particular relevance for river regulation, more research focus on cultural services, which are often viewed as incommensurable (Muradian & Gómez-Baggethun, 2021), might help to build broader societal consensus about how to make policy decisions in potentially trading off salmon ES for carbon-free power production.

Out of the four categories of ES, cultural services have been the most difficult to incorporate into assessment methodologies (Liu et al., 2019; Lynch et al., 2016). We found few articles that explicitly assessed or implicitly considered cultural services—somewhat surprising perhaps, given the salmon's status as the “king of fishes” for centuries. Salmon clearly bear non-monetary meaning to many people, and they have done so for centuries, although contrary to the Pacific salmon (Bottom et al., 2009), the aboriginal relationships to Atlantic salmon are less well documented in the scientific literature (e.g. Denny & Fannig, 2016). Although Atlantic salmon conservation has been a focus of ecologists, anglers and river managers for decades, we seem to have until recently done a poor job of accounting for the diverse values of salmon for policy makers and the general public (Myrvold et al., 2019). The concept of ecosystem services has been at the forefront of nature conservation policy for nearly 20 years now, but our results suggest that salmon scientists have done relatively little to engage with ES. Our study shows that applied research and interdisciplinary tools that can assess the diversity of services and values of salmon should be used more often. Moreover, since different methods for assessment show different and partial values of the services assessed, river ecologists need to engage further with how the ES framework and methods represent the importance of particular species. Focusing on non-monetary aspects of ES valuation can have the added benefit of developing more inclusive management involving stakeholders with diverse worldviews (Brondizio et al., 2019; Rozzi, 2012), for example, ecocentric values that find salmon as loci of value (Mueller, 2017; Piccolo, 2017) which may be powerful motivators for conservation (Piccolo et al., 2018). A rights-based approach to sustainable use of salmon populations, encompassing multiple ways of viewing the world may facilitate legitimate conservation actions (Díaz et al., 2018).

Using a set of databases through the Web of Science, our literature search was limited to scientific publications in English. Therefore, we may have missed some sources of information that discuss the connection between ES from salmon and hydropower, particularly those with a focus on indigenous culture. Additionally, there may be relevant information in the grey literature and in languages other than English. Including this body of literature in future work would likely contribute to new insights into the relations between salmon, hydropower and people. On the other hand, using a systematic literature search creates transparent and reproducible results, and our results reflect the research community's current state of knowledge about ES from Atlantic salmon and hydropower.

Even if fisheries researchers have thus far been limited in explicitly describing the effects of hydropower on ES delivered by Atlantic salmon, the case is clear that damming and habitat alterations have had far-reaching negative effects on salmon populations (Dymond et al., 2019; Erkinaro et al., 2011; Forseth et al., 2017; Lenders et al., 2016). Thus, river managers are likely to be increasingly called upon to alter hydropower planning and operations (or even to remove dams) to improve fish passage and instream habitat. On both sides of the Atlantic, regulations such as the Endangered Species Act (USA) and the Habitats Directive (EU) are already in place that requires river managers to conduct such remedial measures. In Sweden, where most of the authors of this article work, all hydropower plants will be relicensed in the coming decades, for example, and this process will include assessing trade-offs among competing interests. It is worth noting that most such policies and laws apply to all riverine fish species; our focus on Atlantic salmon may be of some guidance, therefore, in developing ES assessment frameworks of lesser-known species. In any case, river managers can likely gain broader public support for conservation and restoration measures by engaging with stakeholders and adding ES assessment methods to their toolboxes.

The coming decades are likely to see a radical change in how natural values are assessed at the international level, with the concepts like ES and the IPBES' Nature's Contributions for People leading in the policy arena. It is high time that salmon researchers get on board by explicitly addressing the diverse values of salmon, in particular when trade-offs exist between services provided by salmon and hydropower.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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